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CORRELATION OF TAXONOMIC AFFINITIES WITH FOOD HABITS IN HYMENOPTERA, WITH SPECIAL REFERENCE TO PARASITISM¹

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ENTOMOLOGISTS can all agree that the attachment of most phytophagous species belonging to the more highly specialized orders of insects is very firmly fixed, and the Hymenoptera form no exception. We can also agree, although in less definite terms, that many parallels exist among plant-eating Hymenoptera between taxonomy and food habits. I do not propose to treat of this series, however, partly because I am not sufficiently familiar with them, but also on account of the great interest which attaches to the parasitic groups of Hymenoptera.

During the last decade our conception of the process of nutrition in insects has undergone considerable change, due to the discovery that various microorganisms form an important part of the food supply of many forms. It is quite certain that certain saprophagous, sarcophagous and coprophagous ones probably feed directly, not at all upon decaying and fermenting plant materials, carrion or excrement, but upon the bacteria, yeasts, etc., always abundant in organic material undergoing decomposition. We must judge of the protein requirements of such insects not by the gross substances or substratum, but on the basis of the microorganisms present (Baumberger, '19).

This aspect does not appear to enter into the economy of the Hymenoptera, although there may be a relation between fungi and nutrition in some Cynipidæ, as the

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galls of these insects are commonly invaded by fungi and yeast-like organisms. On the other hand, these same gall-wasps exhibit remarkable correlations between structure and habits as shown by many workers, most elaborately and clearly by the recent studies of Kinsey ('20). The Cynipidæ are at present restricted to a very limited series of plants on which they induce the formation of galls. With the exception of some undoubtedly primitive forms, they occur almost exclusively on Rosaceæ of the genera *Rosa* and *Rubus*, and on the unrelated genus *Quercus*, the latter harboring a very large number and a far greater variety of forms. In the gall wasps, we see, therefore, a nearly exclusive association with a very few genera of plants and what is still more striking is the fact that the more primitive ones, although few in number, exhibit a wide range of food-plants. This leads to the inevitable conclusion that we can trace the evolution of host relations in this group as now living, from a very generalized condition to a highly specialized one.

Many other insects, particularly Homoptera, harbor certain probably symbiotic organisms, and recent studies (Brues and Glaser, '21) tend to show that these may be very important factors in the nutrition of the insects. Almost nothing is known concerning such organisms in Hymenoptera, but if they are present in some cases, as seems probable, they must be reckoned with in any complete studies of food-habits.

The relation of food-habits to taxonomy in the Hymenoptera becomes particularly interesting in connection with the appearance of parasitism in several forms, which is of widespread occurrence in the order. In fact, a large proportion of the Hymenoptera are parasitic, and with the development of this mode of existence have come such elaborate structural modifications, and specialization in behavior, that species have multiplied at a very rapid rate. From this apparent chaos, even taxonomists have as yet brought only very partial order, and any discussion of parasitism in the Hymenoptera is

necessarily very incomplete and may be misleading in some details.

In the Hymenoptera the designation "parasitic" has been applied to habits of extremely diverse nature, and this very loose use of the term may easily lead to serious confusion unless we consider the matter carefully before proceeding further. It is most commonly applied to several large and abundant groups whose members live in the larval condition in other insects which they almost invariably destroy after attaining full growth. Such habits are quite similar to those encountered in other orders of insects, although in no other do they attain such a high degree of specialization; nor do they involve such a series of unrelated smaller groups, with the possible exception of the Diptera. While this is the most abundant and widespread type of parasitism among insects, we must not lose sight of the fact that it is a rather unusual condition so far as animals and plants in general are concerned, in that the parasite and host belong to the same class and are thus closely related. A similar relation exists among the Crustacea where certain decapods are parasitized by other members of the same class, and even among Protozoa there are ciliates parasitic in the bodies of other infusorians. Such associations are very rare, however, and the vast majority of parasitic Crustacea and Protozoa, as well as other parasitic animals, depend upon animals far removed from themselves for hosts, although there is very generally a close correlation between the host and parasite in that related parasites depend upon related hosts. Another peculiarity of this type of insect parasitism lies in the prompt death of the host, which does not usually ensue as a result of other animal parasites, although it is a common result of presence of some protozoan parasites of the higher animals. In others, again, like the well-known nematode, *Trichina*, the ultimate death of the host is necessary for the continued propagation of the parasite, but actual death normally results from other causes. Still another charac-

teristic of this type of insect parasitism is its restriction to the larval stages, although extending over the entire growth period. This is by no means unique among animals, but it is one of the distinguishing characteristics between this type of parasitism and the one next to be considered. In its perfected state this relation between host and parasite is a marvelously balanced association and one which we might expect to furnish valuable data on the correlation between taxonomy and habits.

A second type of parasitism encountered in the Hymenoptera is that exemplified by most of the parasitic bees and wasps. This has recently been discussed by Wheeler ('19). Here the parasitic larva is really at first predatory so far as food-habits are concerned, devouring the host larva shortly after hatching. The sequence of events is initiated by the preparation of the larval food-supply of the host by the mother bee or wasp. Most solitary wasps store up, in a nest which they have prepared, one or more insects which they have paralyzed by means of the sting, and attach one of their eggs to the body of the prey. Under normal conditions the larva hatching from this egg consumes the prey, attaining full growth, and later completing its metamorphosis. Bees behave in much the same manner, but the store of food in the nest consists of honey and pollen. When parasitism intervenes, the egg of the parasite is also placed upon the food supply, and on hatching, the larva of the host and parasite find themselves in proximity, each ready to appropriate the contents of the nest. In numerous cases that have been studied (Graenicher, '05), the larva of the parasitic form has more powerful jaws than its rival, and encounters little difficulty in destroying it. It now proceeds to consume the food-supply exactly as the host larva would have done, casting off its enlarged mandibles at the first molt. Thus the actions of the larva savor not at all of parasitism, but it is in the fixed habits and instincts of the adult, which require the nests of particular wasps and bees, that the parasitic relation holds.

Correlated with such habits, structural modifications of the body appear, such as the loss of the pollen-collecting apparatus in parasitic bees.

In certain ants there occurs a third type, social parasitism (Wheeler, '04) whereby the young females of some ants that do not establish their own colonies insinuate themselves into the nests of other species of ants, do away with the queen, and take on themselves the function of egg-laying. As the larvæ from these eggs are raised to maturity, they produce worker individuals of the parasitic species which gradually supplant the original population. Finally, the colony becomes pure and maintains itself through its own efforts, giving no evidence of the temporary social parasitism by which it has originated. In a very few cases social parasitism may become permanent with the complete elimination of the worker caste.

The term entomophagous parasite may be applied with some appropriateness to all of the three types described, but is most suitable for the first one, since there the parasite not only consumes its host, but feeds upon nothing else during its developmental stages. By far the largest number of species in the order exhibit this type and it is the only one which I shall consider in any detail.

There are several ways in which such parasitism may have originated, but the question of origin is best deferred until its several phases have been discussed at greater length.

Defining parasitism in its several forms as enumerated on a previous page, we find that there are parasitic genera included in nearly all of the larger groups of Hymenoptera. Thus, the Ichneumonoidæ, Serphoidea and Chalcidoidea, each represented by a number of families, are almost exclusively entomophagous parasites, while in the Aculeata, numerous parasitic genera appear, scattered through a series of families with generally non-parasitic habits. In addition to these there is the primitive family Oryssidæ, now known definitely (Rohwer,

'17) to be parasitic, and a few other families nearly all of somewhat doubtful affinities. Thus of the nearly one hundred families included in the order, between forty and fifty are composed either entirely or almost exclusively of genera with parasitic habits, the remainder being phytophagous or predatory with isolated cases of parasitism, among both the predatory series, and one of the phytophagous ones.

Considering these larger groups, the suborders and superfamilies, more in detail we find that the most primitive of all known Hymenoptera, the suborder Chalastogastra, are phytophagous. Of these, about a dozen families, comprising the sawflies or superfamily Tenthredinoidea, are almost exclusively defoliating forms, feeding in their larval stages on the leaves of various flowering plants. Another family, the Siricidæ, feeds internally on the tissues of woody plants, and, at least so far as food-habits are concerned, there are two other families which form a transition between the sawflies and wood-wasps. It is in the groups above these that the parasitic habit appears, and with the possible exception of one family, the Oryssidæ, to be mentioned later, all these groups are usually associated as a second suborder, Clistogastra, contrasted to the more primitive Chalastogastra. Among them several groups of families, conveniently classed as superfamilies, are three extensive parasitic ones: first, the Ichneumonoidea, comparatively large species comprising about half a dozen families; second, the Chalcidoidea, represented by small or minute species comprising fully a dozen families; third, the Serphoidea another half dozen, mainly very small species. Together with a part of the Cynipoidea, these form the enormous complex commonly known as the Hymenoptera Parasitica. All are quite closely related, but rather easily grouped and distinguished, in spite of certain annectant and aberrant families.

The habits of the several series are also very uniform.

The egg is nearly always laid upon the body of the host or thrust into it, usually the latter, to which purpose the extrusible, stiletto-like ovipositor of the female is adapted with great nicety. Oviposition may take place either in the egg of the host, in the larva, or even in a later stage, and the parasite may complete its development either in the stage of the host in which it is laid, or development may be delayed and not completed till the host has proceeded to a further stage in its ontogeny. Under such conditions the larva is to a great extent passive, although in its earlier minute stages it frequently exhibits (*e.g.*, in certain Serphoidea) great modifications in body form, and develops monstrously specialized jaws or other organs to aid in attacking the massive tissues or yolk-masses of its host.

When such modifications of the young larva are transitory and disappear almost completely after one or two ecdyses, they form a transition to several very clearly defined cases of hypermetamorphosis which have been noticed in certain Chalcidoidea by several observers (Wheeler, '07; Smith, '12, and Brues, '19). In members of two families, the Eucharidæ and Perilampidæ, they have found an active, free-living, first stage larva known as a planidium which is quite similar to the triungulin of the Meloid beetles and the Strepsiptera. Like them, the planidium becomes helpless once it has become parasitic. Great interest attaches to the planidium, but until its distribution is much better known it can not be considered of taxonomic value, especially as quite similar larvæ are known in several other orders of insects. Another series of Hymenoptera, certain parasitic bees, are known through the researches of Graenicher ('05) and others to possess much larger jaws in the first larval stage. As we have mentioned previously, the type of parasitism in this case is very different, for the parasite simply eats the host larva that it may appropriate its food-supply, and we have a parallelism in structure, of

independent origin, and hence of no classificatory importance.

Comparative anatomy and post-embryonic development show very clearly that, with the exception of some secondarily phytophagous forms, only the primitive Hymenoptera are phytophagous. As one can not seriously question the monophyletic origin of the order, the varied food-habits now represented must have been derived from some form of vegetarianism.

In all of the higher Hymenoptera or Clistogastra, active and aggressive characteristics are very prominent in the behavior of the adult females, whatever may be the food-habits of the larvæ. Thus in the wasps, the parent captures as prey suitable insects with which to feed her larvæ, or to provision her nest, if her young are to receive no post-natal care. In all cases she prepares some sort of a cell or nest for her brood, and frequently this requires marvelous skill in the selection of particular materials and the collection of specific insects for food. Where nests are provisioned in advance, the prey is stung and paralyzed after a manner that requires very complex instinctive behavior. If, on the other hand, we look at the activities of the larva of one of the wasps that stores a paralyzed insect away and places her egg upon it, we see the larva consuming its food supply much after the fashion of an externally feeding entomophagous parasite. In fact, it is difficult to distinguish any really fundamental differences. In each case the host is stung and the egg attached to it, always externally by the wasp, but sometimes externally also by the parasite. The wasp paralyzes her prey, which the parasite does not do, as her sting is not so severe, and she does not further bother with the host insect. The egg of the parasite is deposited at the time of stinging, and that of the wasp by a later operation of the same organ, the ovipositor with which she has previously paralyzed, but not killed, her prey. Thus, aside from the maternal instincts, the entomophilous wasp is scarcely more different from the ichneumon-

fly, than some ichneumons from others.² Equally varied habits exist in at least a few cases even in a single species of ichneumon, for certain *Itopectis* may be either parasites of caterpillars, hyperparasites, or inhabitants of the egg-cocoons of spiders where they devour the contained eggs. From the entomophilous wasp has been developed the parasitic one and we have alluded to its origin as traced by Wheeler ('19).

From the foregoing, it is seen that we might derive the habits of the wasp from those of the parasite, or *vice versa*, with but little difficulty, although the more elaborate instincts of the wasp appear more naturally as the latter development.

If now we return to the free-living phytophagous *Chalastogastra*, it appears for morphological reasons especially that the entomophagous ichneumon flies have been derived directly from them and I think that the transition from phytophagy to parasitism is quite clear. Whether it involves the interpolation of predatism or sarcophagy is perhaps more a matter of conjecture.

The *Siricoidea* of the *Chalastogastra*, on account of their legless, eruciform, lignivorous larvæ and reduced wing venation appear to have been derived from some sort of ancestor with a caterpillar-like larva having the more complex wing-venation seen in the saw-flies or *Tenthredinoidea*. So far as is known, no member of either group is parasitic. Until recently the family *Oryssidæ* has been regarded as a degenerate group quite closely allied to the *Siricidæ*. Rohwer has, however, shown that they are really very different and finally (Rohwer, '17) regarded them as a distinct suborder of Hymenoptera. It seems reasonable to suppose that they have *Siricid*-like ancestors, and as they are now known definitely to be parasitic on the larvæ of wood-boring *Coleoptera*, it ap-

² This matter, as well as several others discussed in the present paper, have been recently dealt with by Picard in a publication (*La faune entomologique du figuier*, '19) which I unfortunately did not see until too late to refer to it in the text of this article. Picard's "Considérations sur les parasites," pp. 166-172, are of extreme interest.

pears that we have in them the most primitive parasites in the order Hymenoptera. The hosts of the Oryssidæ consist partly, although probably not entirely, of *Buprestidæ*, which paleontology shows to be an ancient family. Handlirsch ('08) has even gone so far as to suggest that the parasitic Hymenoptera may have been derived from the Jurassic *Pseudosiricidæ* which no longer laid their eggs in wood, but in the eggs of beetles occurring in the wood. This is entirely speculative and so I think must be at the present time any suggestions as to how the Oryssidæ, or the *Ichneumonidæ*, which Handlirsch had in mind, became parasitic. That their larvæ first found and fed upon their hosts after hatching seems much more probable. It must be said, however, that predatory or carnivorous *Chalastogastra* are not known among living forms, except certain adult sawflies which fed in this way (cf. Mrázek, '09). From this point onward we have little trouble in tracing the probable origin and relationships of the *Ichneumonoid* families as I have attempted to do in a previous paper (Brues, '10). Thus the *Stephanidæ* are structurally primitive and strikingly like the Oryssidæ in the peculiarly horned head which had been remarked on before the habits of the Oryssids were known. On account of the presence of a costal cell in the wing, the polymorphic family *Evaniidæ* is necessarily also more primitive than the *Ichneumonidæ* or *Braconidæ*, and, through one subfamily, the *Fœninæ*, resemble the *Stephanidæ* as has been already noted by Bradley ('08). Some *Braconidæ*, the *Stephaniscinæ*, *Spathiinæ* and *Hormiinæ* are much like *Stephanids*, so much so that it is difficult to believe that they are not directly derived from them. One other family, the *Capitoniidæ*, recently segregated from the *Braconidæ*, appears to be very definitely related to the more generalized *Evaniidæ* (*Aulacinæ*). Omitting in this brief consideration several less pertinent families, and ignoring other recently segregated ones, we have left only the *Ichneumonidæ*, related possibly through the *Alysiidæ* to

the Braconidæ. Structurally this relation seems plausible, but as the Alysiids attack almost exclusively the highly specialized Diptera it is very difficult to regard them as closely related to the ancestors of the Ichneumonidæ, so highly diversified in habits and structure. The latter then are not so easily derived and may go back to Evaniid-like forms.

One extremely interesting fact in connection with the primitive families of parasitic Hymenoptera is their association with wood-boring insects. Thus the Oryssidæ, the most generalized group of Evaniidæ, the more primitive Braconidæ, many of the structurally primitive Ichneumonidæ, and the Capitoniidæ are restricted to hosts having such habits. This shows undoubtedly that such habits have not easily been changed and that similarity of host-habits is an important factor in determining what insects may be attacked. This supports strongly our thesis of the interrelation of taxonomy and habits.

In connection with the parasitism of certain chalcid-flies, the French entomologist Marchal ('98) discovered, some years ago, a most anomalous method of precocious multiplication which he designated as polyembryony or germinogony. In species exhibiting this phenomenon, the embryo becomes dissociated into a large number of parts, and from the numerous germs thus produced there is formed a veritable swarm of minute parasites, the extent of which is limited only by the available food supply in the host. Marchal's first observations have been much extended since by himself and numerous other workers, and the same condition has been found to exist in many other Chalcidoidea and also in the Serphoidea (Marchal, '03). It has recently been recognized in another widely different family, the Dryinidæ by Kornhauser ('19) and probably occurs sporadically in several other parasitic families, although I believe no other cases have been absolutely substantiated. From the regular association of numerous individuals in single hosts in the case of *Microgaster*, allied genera of the Braconidæ,

and in *Sphæropyx* (Cushman, '13), in a few Ichneumonidæ (e.g., species of *Cryptus*) and in a few Bethylidæ, it would seem likely that they also are polyembryonic.

The widespread occurrence of germinogony and its apparently erratic distribution show that it can be of no general taxonomic interest at least as an aid to classification. It is indeed quite the opposite, for the development of the egg in the process of fragmentation is so similar in the Chalcidoid and Serphoid that we might be led to believe it of common origin. As their ancestors were undoubtedly not polyembryonic, such can not be the case and the process must have originated independently, just as it has in several totally unrelated animals like certain annelids (e.g., *Helodrilus*) which exhibit it in an imperfect condition (Weber, '17) and in the armadillo (Newman and Patterson, '10) among mammals where it has become completely established. A quite similar modification of development is seen in the formation of the rediæ in the sporocysts of Distomes. Still similar, but delayed until the larval stage, is the process of pædogenetic multiplication in the Cecidomiid fly *Miastor* (cf. Felt, '11), well known to all entomologists.

It appears from any general survey of the habits of the parasitic Hymenoptera that we find certain taxonomic groups of host commonly attacked by discrete groups of closely related parasites. It is natural that such combinations should impel our attention, as they may be fitted with the least effort into a classified scheme, and furthermore their mere recurrence is sufficient to indicate that they are not due merely to chance.

The following list includes a few striking instances of this sort drawn at random from widely separate sections of the order:

Parasites	Hosts to Which They are Restricted
Families	
Alysiidæ	Dipterous larvæ.
Trigonalidæ	Vespidæ.

Subfamilies

Evaniinæ	Cockroaches and their oöthecæ.
Ichneutinae	Saw-fly larvæ.

Genera

Polygnotus	Cecidomiid larvæ.
Coccophagus	Soft scales.

If we should reverse the order of the above list and attempt to tabulate groups of related hosts that are affected only by certain groups of parasites we should have great difficulty in finding examples. This, of course, is to be expected on account of the passive condition of the host and the active rôle of the parasite, whereby it first came to infest some certain kind of host. Inheritance of such specific instincts over long periods of time, during which groups were becoming differentiated, will lead naturally to the evolution of groups of parasites attached to groups of hosts which have meanwhile been developed. Such reasoning appears to be sound and may explain some of the conditions tabulated above.

I think, however, that there is a deeper basis than this, and that we can not fully understand such combinations without inquiring into the actual physiological relations between host and parasite.

It has been customary among entomologists to place great emphasis upon the maternal instinct of invariable selection as determining and restricting the range of hosts affected by specific parasites. Among zoologists who deal with other parasites, particularly Protozoa and lower invertebrates, no such idea has ever been entertained, as the parasite plays a passive rôle in attaining its host. The malarial parasite is ingested by all insects that suck human blood, but is able to continue its parasitic life only in certain particular mosquitoes. Similarly, a certain Cestode worm parasitic in birds has as intermediate host, the garden slug, from which the definitive host obtains it by eating the slug. That this Cestode does not occur in other hosts that may eat infected slugs is a phys-

iological matter and is always regarded as such by helminthologists who encounter many instances of this kind. On account of the definite requirements of such parasites, Cobb ('04) suggested some years ago that they might give valuable clues to the taxonomic affinities and physiological peculiarities of their hosts, the latter particularly in cases where there is a wide range of hosts.

In insects, and, quite fortunately for the present discussion, in the parasitic Hymenoptera, there are available some extremely pertinent observations made by Timberlake ('12) relating to the fate of eggs in the bodies of host insects in which they do not normally develop. His experiments were made with an Ichneumonid, *Linnerium validum*, commonly parasitic in caterpillars of the fall web-worm. This parasite will also oviposit in larvæ of various other moths, when persuaded to do so in captivity, by depriving it of its normal host; but it can not complete its development in the experimental hosts. This is due to the death of the young larvæ, which succumb to the reactions of the host soon after hatching, or possibly in some cases even before hatching. The antagonistic action of the tissues of the host is manifest by the accumulation of amœbocytes about the unwelcome objects. In one other abnormal host, the tent-caterpillar, this *Linnerium* may survive and complete its transformations, but there is a high mortality among the parasites, for many are destroyed by the host.

These experiments show very clearly why this parasite is restricted to certain hosts and, from the nature of the reaction, which is so similar to that exhibited by animals in general toward microorganisms and other foreign materials, there is little reason to doubt that insects usually react in this fashion. This also furnishes an explanation for the continued restriction of parasites to specific hosts, based upon natural selection, since individuals choosing unsuitable hosts will suffer a very material reduction in the number of their immediate progeny. This is, I think, especially important, as it takes much of the burden from

the already greatly strained principle of the fixity of instinct in the imaginal insect.

It also aids greatly in understanding the relation previously referred to, where extensive groups of parasites attack discrete groups of host. Adaptation to one host means ordinarily greater physiological suitability for another closely related host than for a widely different one. This, no doubt, applies to cases like the Alysiid parasites, for here the series of hosts, while quite uniform, is so extensive that it can not be explained on the slowly acting basis of concomitant differentiation of the hosts and parasites.

Instances, like one cited by Pierce ('08) where several species of parasites suddenly became abundant enemies of the boll-weevil due to the scarcity of their more favored hosts, must depend upon selection, as suggested above, leading to the rapid improvement of partial adaptations.

We have already referred to the fact that the parasitic Hymenoptera, and quite generally also most parasitic insects, attack other insects, and pointed to this as a characteristic more or less peculiar to insect parasitism or at least to its most prevalent types.

The attachment to closely related animals as hosts is shown still more clearly in Hymenoptera that are secondary parasites on parasitic species of the same order, of the same family, or even of related genera. This phenomenon is not restricted to Hymenoptera, but is most extensively exhibited by them. Thus certain genera of Ichneumonidæ, Braconidæ, and Chalcidoidea develop regularly in the larvæ of primary parasites which become established in a free living host.

Secondary parasites are not absolutely distinct from primary ones in some individual cases, for this relation is known to be facultative in a few species of Hymenoptera which develop in either way. In 1903, Fiske ('03) showed from careful breeding experiments that certain Ichneumonidæ of the genus *Itoplectis* may be either pri-

mary or secondary parasites of the tent-caterpillar, attacking a member of their own family in the latter case. Since then other examples have come to light, but they are by no means common. Another fact which is significant in connection with secondary parasites is that they are very generally much less particular than primary ones in restricting themselves to a small series of hosts.

In searching for the origin of secondary parasitism, it is certain that it must be derived from the primary form, since it is naturally dependent upon the latter for its mere existence. The only other possibility appears to be the assumption that the primary parasites were free-living forms when first parasitized, and that they have since developed parasitic habits of their own. As the secondaries are frequently structurally reduced such a supposition appears still more improbable.

If, then, secondary parasites are derived from primary ones, what can have caused them to desert their free-living hosts? We have already seen how the restriction of hosts among primary parasites seems to have a physiological basis, in that the reaction of the tissues of the host has been shown (Timberlake, '12) to eliminate parasites not adapted to it. In attacking insects very closely related to themselves parasites should stand a much better chance for successful growth, as the physiological antagonism of all animals toward closely related forms is much less than that toward very different ones. Young larvæ of parasitic species should therefore meet with less difficulty in developing in the bodies of related forms, and secondary parasitism might arise with little difficulty when eggs were placed in another parasite rather than in the body cavity of the free-living host. This explanation may account for the prevalent type of hyperparasitism, but not for cases like that of the Chalcidid *Dibrachys* which attacks Hymenoptera and Diptera alike. This may simply be a case of great adaptability in certain species like some mentioned in connection with pri-

mary parasitism, although it may depend upon a general similarity in the tissues of all entomophagous parasites, or a less aggressive condition of the tissue in parasites due to their generally secluded and protected environment. As the latter condition seems not unlikely, it probably acts regularly to make hyperparasitism an easily acquired characteristic.

Striking divergencies, like the following, noted by Swezey ('08), are of interest in this connection. In his studies of Dryinid leaf-hopper parasites, he found a Ceraphronid parasitic on a species of the related Dryinidæ, although the group normally and abundantly parasitizes entirely different types of insects.

The adaptation of animals and plants in conformity with the demands of diverse environmental conditions is now an axiom among biologists. From its manifestations it is evidently a physiological adjustment which leads secondarily to structural changes, and many convergences in form and function are traceable to it. On account of the close interdependence of plants and insects it appears, in some instances at least, to exert an indirect influence upon phytophagous insects (Brues, '20), whereby a species may feed rather indiscriminately on herbs, and another on woody plants, but not upon the two in combination.

In the case of parasitic Hymenoptera there are many instances which might be cited where environment appears to have exerted a direct influence upon the acquisition of host relations and others where we must, I think, believe the influence to be indirectly related to the environment through a second insect, the host. This rather obscure statement may be clarified by a few examples. From what we have said in connection with hyperparasitism, it seems quite clear that a species which may assume the rôle of either a primary or secondary parasite, responds quite directly to the environment, in this case the primary host, which may be either sound or already infested by a parasite which is in turn at-

tacked. This influence seems to be a rather direct one. On the other hand, I may quote from a previous paper (Brues, '08) the following: "The European Chalcid-fly, *Ormyrus tubulosus*, has been minutely studied by Mayr, who has bred it from no less than 27 species of Cynipid galls, and I have from Massachusetts what is apparently the same species, bred from about half as many North American species by the late Dr. M. T. Thompson. The galls formed by the various hosts of this species are many of them entirely dissimilar in form, the only resemblance between them, aside from their gross gall-like form, being their more or less uniform habitat attached to twigs and leaves." Howard ('91) mentions *Enrytoma rosæ* as having over 50 cynipid hosts. A range of hosts of this sort appears to be due not directly to the environment of the host, but to the similar physiological condition of the various Cynipids themselves, which, as we have already said, are closely confined to a very narrow range of food-plants.

The great difficulties occasionally imposed upon parasites in attaining their hosts may be purely a matter of environment, as illustrated by the following considerations.

An interesting series of parasitic Hymenoptera are those which prey upon aquatic insects. In several well-known cases, the behavior of the adult parasites has become so profoundly modified that the females not only enter the water in search of their hosts, but they may be, occasionally at least, accompanied by the males. The first observation of this sort was made nearly a century ago by Francis Walker ('36) on *Agriotypus*, and the well-known observer Sir John Lubbock ('63) later gave an account of the habits of two aquatic Chalcis-flies in which he describes the actual process of swimming. One species, the Mymarid (*Cataphractus cinctus*) makes use of its ciliated, paddle-shaped wings for this purpose, while the other, a Trichogrammid (*Prestwichia aquatica*) propels itself by means of the legs. Numerous other contribu-

tions, notably those of Von Siebold ('58), W. Müller ('89), Marchal ('00), Rousseau ('08), Heymons ('08), Schulz ('07, '10^a, '10^b), and Matheson and Crosby ('12), have added much of interest, not only in bringing to light aquatic members of several families, but in determining some of the host species upon which they prey. In many cases the adaptation to aquatic life is not so perfect as the cases just mentioned, although several other species are known to swim readily, using either the legs or wings, which usually show modifications adapted to such behavior.

In view of the frequent occurrence of aquatic imaginal forms in other orders of insects such as the Coleoptera and Hemiptera, it is perhaps not surprising to find certain parasitic Hymenoptera adopting this habitat. Viewed more in detail, however, the matter is quite a different phenomenon. Such Coleoptera as Gyrinidæ, Hydrophilidæ, Dytiscidæ, etc., are uniformly aquatic in both preparatory and imaginal stages, and such is also true of the brachycerous Hemiptera. All of these insects are highly modified to conform with their aquatic environment, particularly in reference to the functions of locomotion and respiration.

In the aquatic Hymenoptera, a series of families is represented and only a comparatively small number of genera are included. The structural modifications are far less profound, indeed they frequently represent very slight changes. They are more closely parallel to the natatorial habit shown in isolated genera such as the rice water-weevil, *Lissorhoptus simplex*, a beetle that has become aquatic and oviposits in the roots of the rice plant (Tucker, '12). It has been shown experimentally by Szymanski ('18) that many terrestrial insects may be induced to swim if submerged and we may easily suppose that the truly aquatic habit of the parasitic Hymenoptera just mentioned may have arisen through the seeking of their hosts in aquatic plants, first at or above the surface of the water, and later through a search for further indi-

viduals below the surface. Even memory could easily play a part here, if the host were submerged during the development of the parasite, and the latter emerged as an adult below the water, from which it must escape by locomotion through the water.

In the case of aquatic Hymenoptera, it is readily seen that we can not correlate taxonomy with habits according to any generalized scheme, although the several genera show structural characters associated with their unusual habits. Most striking is the number of Mymaridæ and Trichogrammatidæ included, minute insects whose wings are naturally well suited for swimming.

Frequently a secluded habitat acts as a powerful factor in restricting the kinds of parasites that can attack certain types of hosts. Thus, wood-boring insects can be reached only by species provided with long ovipositors. Such restrictions are clearly defined and many other examples might be cited. Partial inaccessibility of the host may even occur in the case of parasites otherwise well suited to their host, as for example in the case of a common parasite of the eggs of the gipsy moth, which is able to oviposit only in the eggs occupying a superficial position in the egg-mass of the host. Sometimes difficulties may be overcome by the presence of an active first-stage larva. This may exhibit most extraordinary behavior as has been described by Smith ('17) in the Chalsis-fly, *Perilampus*. Here the *Perilampus* egg is deposited and hatches away from the body of the host as a planidium which later attaches itself to the host and remains there till the host completes its growth, after which the planidium begins its parasitic life. A second species that is a hyperparasite seeks out the primary parasite in the caterpillar host through which it bores its way and there awaits the exit of the primary parasite before proceeding with its development.

Again, the female of some egg-parasites attach themselves to individuals of the host species and are thus carried to the place where the eggs within which they will

develop are to be deposited. Certain Chalcids-flies and Serphoids have adopted this curious method of transportation (Brues, '17) which occurs sporadically in diverse insects (Banks, '11). The way in which many modifications of this kind appear in similar form makes it impossible to consider them as guides to taxonomic affinity. The elongated ovipositor, the active first-stage larva, and many other adaptations for attaining the host are of course good taxonomic characters, but they reappear independently in more than one group, and can be used only in combination with characters of less vital importance to the animal, to characterize completely any extensive groups. Nevertheless, the lengthened ovipositor can be used to separate numerous families and smaller groups in the parasitic Hymenoptera and as it bears a certain relation to habits, the latter are thus reflected in taxonomy on a structural basis. However, the habits of many such insects do not seem to require such a long ovipositor and represent not the primitive habit for the group, but recent modifications which break down the homogeneous correlation of structure and habits.

Closely connected with the specific association of natural groups of hosts and parasites is the great variation shown by different parasites in the number and diversity of the species that serve as their hosts. Just as we can find among phytophagous insects, omnivorous forms, strictly monophagous ones, and all intergrades between the two, so there exists among parasites an almost equally varied series of associations with one, several or many hosts.

Although parasitic Hymenoptera are so abundant, both in species and individuals, their food habits are not so easily observed as those of plant-eating insects and our knowledge concerning them is far less complete. The large number of secondary parasites also lead to confusion, as these may not always be distinguished on a structural basis.

If parasitism demands a nice physiological adjust-

ment, we might expect to find that egg-parasites affecting the organism at an earlier and less highly differentiated stage of ontogeny, are more catholic in their tastes. This is, however, not borne out by observation to any extent, and egg parasites are usually as closely restricted to particular hosts as their relatives who confine their attention to larval insects.

Small size is a prerequisite of all true, internal egg-parasites except a few that occur in the oothecæ of cockroaches, where the comparatively large species of *Evania* undergo their development. Some parasites oviposit in the host-egg, but live at the expense of the larva; they are, except in polyembryonic forms, larger, and not classed as egg-parasites.

On the basis of size, then, practically all egg parasites are either Chalcidoidea or Serphoidea and this habit characterizes a number of families, and smaller taxonomic groups (cf. Girault, '07, '11). Among them the strange, tropicopolitan genus *Podagrion* attacks only the eggs of Mantidæ. The large cosmopolitan genus *Teleonomus* occurs in the eggs of various insects, mainly Lepidoptera while the very similar genera *Phanurus* and *Trissolcus* are restricted to eggs of Tabanidæ and Pentatomidæ. Again, *Scelio* and several related genera attack only the eggs of the Orthoptera Saltatoria. Thus, if used with due caution, egg-parasites are in the main illustrative of close correlation between the taxonomy of host and parasite in spite of the fact that we may naturally regard insect eggs as more similar *inter se*, than insect larvæ.

It is true that the ubiquitous little *Trichogramma* affects eggs of several orders and many families of insects, but like other less conspicuous examples, it stands quite apart from its commonplace associates.

With their larger and more variable size, and great diversity in habits and structure, larval insects present a correspondingly varied series of opportunities for parasites. We find also that practically no genera are known

to parasitize both eggs and larvæ, although the polymorphic and widespread *Eupelmus* among the Chalcid-flies appears to be an exception. As the eggs and larvæ of many insects frequently occur together at the same time, this fact is rather surprising and shows that the parasitic association must depend greatly upon gross form, as well as upon the factors of environment and specific physiological reactions, which we have already mentioned. One case which comes to my mind in this connection is quite instructive and there are no doubt others of a similar nature. All the several genera included in the Evaniinæ are, as previously mentioned, parasites in the egg-cases of cockroaches, with the exception of a single reliable record (Picard, '13) of the rearing of *Zeuxevania* from the body of the blattid itself. Quite likely the future may bring forth other similar observations on Evaniines, but this one shows that parasitism has been transferred to the cockroach from the oötheca, which is of course carried about by the female for some time before deposition.

Larval parasites have been more extensively reared than those living in eggs and their habits are consequently better known. Many observations upon individual species of hosts show that the larval stages harbor a far more extensive series of parasites (*e.g.*, Howard and Fiske, '12) than the eggs or pupæ, while hymenopterous parasites of the adult are almost unknown. Among larval parasites it is easy to recognize two general series, so far as the number of hosts utilized. Some species are very conservative in this respect and others extremely versatile. These two terms are equally suitable for genera and larger groups, and the difference is more important when it involves all or most of the species of quite extensive groups. Thus the highly modified members of the family Dryinidæ (Perkins, '05) are restricted to several families of Homoptera. A few which parasitize Membracids are insects of quite ordinary appearance, but the remainder affecting Tettigoniellids and

Fulgorids have the fore tarsi of the females misshapen to form chelæ or pincers, by means of which they cling to their host. Such structures are elsewhere unknown among insects. The group has become highly specialized, apterous in several genera, and has probably reached the end-stage in its evolution. Like all creatures which have attained this condition, it shows no further adaptiveness in habits. This is a clear-cut case of correlation between habits and taxonomic affinities.

Versatile groups naturally include large numbers of genera and species with varied habits which enable them to grasp every opportunity to earn (or, in the case of parasites, to steal) a livelihood. Numerous species and varied habits, are as inseparable as form and function. The former binary involves an added series of factors, since any group of insect parasites comes into keen competition with the members of other groups as it reaches out for new hosts. Some have spread widely among hosts of very similar types, restrained by some insuperable obstacle, probably physiological in nature, from attaching themselves to strange insects. They show a correlation between habits and structure. Others have broken their fetters more quickly and completely, and adaptations in habit have far outstripped structural modifications, resulting in natural taxonomic groups which show only imperfectly such correlation.

The climax in this direction is reached by certain groups which have cast aside parasitism entirely and become phytophagous. This has occurred independently in several families of Chalcis-flies, a group in which the struggle for existence must be very severe. One of these aberrant series, *Megastigmus* and its allies (Crosby, '13) feed within the seeds of plants, mainly those of various trees, upon a rich protein diet, probably similar to that of their entomophagous forebears. Another, *Isosoma* and its allies (Howard, '91 and '96; Phillips and Emery, '19) occur in far less delectable vegetable tissue, such as the culms of grasses in which they sometimes cause

galls. A third (Mayr, '05), including some genera related to the remarkable parasitic *Perilampus*, which we mentioned a few moments ago, produce conspicuous galls on certain plants.

The production of galls by the phytophagous Chalcids is quite suggestive, since many forms related to *Isosoma* (*Harmolita*) are parasites of gall-making Cynipids. *Megastigmus* also belongs to a group including many parasites of Cynipids. Since we do not know exactly how galls are formed, however, the matter can not be profitably discussed at the present time.

Although they may not aid us greatly in formulating any general causes leading to divergence in habits among related forms, I should like to append a few observations made by various entomologists which suggest a variety of factors.

The effect upon the parasite of almost complete elimination of a host through excessive parasitism has often been commented upon by entomologists. An especially clear case has been described by Aldrich ('12) where an invasion of the western pine-butterfly was suddenly checked by *Theronia fulvescens*. The parasite then found it necessary to eke out an existence from scattering and less suitable forest insects and under such stress, selection must be very keen (cf. p. 147). Complete parasitism of 100 per cent. of the related cabbage butterfly by *Apanoteles glomeratus* has also been reported by Chittenden ('05).

Errors or aberrations of instinct have also been occasionally observed. Thus Marchal ('07) saw a Chalcidid parasite of coccinellids (*Lygellus*) repeatedly oviposit in the pupal exuvia when living material was not available. Still more incongruous is the behavior of *Trichogramma* observed by Holloway ('12) who found this insect actually ovipositing in small globules of partly solidified plant juice on the foliage of okra plants. One of the common hosts of this egg-parasite, the cotton boll-worm, frequently oviposits on the leaves of okra and the globules

were evidently mistaken for moth-eggs. Premature oviposition is generally attributed to physical necessity in relieving the pressure in the body, but here at least it is accompanied by the outward appearance of instinct. Whether this Chalcid tasted the strange new host is not stated, but it is a common procedure among Chalcids (Howard, '10) to tap the host with the ovipositor, and to lap up the exuding body-juices quite independently of egg-deposition. What her reasons for this may be are obscure; possibly it is to test the suitability of the host; perhaps to secure food, or she may even retain a specific appetite for the kind of food consumed in her earlier days.

Marchal, Vayssière ('07) and Loisel ('08) have commented upon the retarded development observed in certain Ichneumon-flies whereby emergence of some individuals was delayed a year. Such occurrences might serve to bridge over the gap of a season when host insects were scarce; on the other hand, if the time were not exactly twelve months it easily might lead to a new "trial" association in the absence of the proper host at that season.

That these factors might lead to divergence in habits, I can not doubt, but hesitate to apply them to any concrete cases of aberrant habits.

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